

Thesis/
Reports
Long,
G. E.

~~Re~~Modeling the Larch Casebearer- Parasitoid-
Host Tree System

WASHINGTON STATE UNIVERSITY

PULLMAN, WASHINGTON 99163

DEPARTMENT OF ENTOMOLOGY

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9 November 1978

Ros

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Dr. Roger R. Bay, Director
Intermountain Forest and Range Experiment Station
USDA Forest Service
Ogden, Utah 84401

Dear Dr. Bay

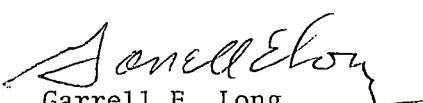
I enclose herein a final report on Supplement No. 21 to Agreement No. 12-11-204-13 entitled:

"Modeling the Larch Casebearer/Parasitoid/Host Tree System".

I am happy to report that we did not spend over \$500.00 of our original budget of \$6668.00. As indicated in the Appendices, the salient features of the study have been submitted for publication in appropriate scientific outlets.

I wish to thank you and the rest of the Intermountain Station, especially RWU-2204, for your support during this study. I hope we can continue to cooperate.

Sincerely,


Garrell E. Long
Assistant Entomologist &
Assistant Professor
509/335-5504

GEL:bb

Enclosure

cc: Ralph Klawitter } Copies delivered
Mal Furniss } at Moscow

Modeling the Larch Casebearer / Parasitoid / Host Tree System

Final Report

to the

Intermountain Forest and Range

Experiment Station

USDA Forest Service

compiled by

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Justification

Recent efforts to construct mathematical models of biocontrol relationships useful for the management of larch casebearer on western larch emphasized a need to specify certain parameters describing aspects of the total system. In some cases parameters had been estimated but confidence in the specified values was low. This lack of confidence arose when, for example, laboratory-derived estimates were applied to field situations, and when model-predicted estimates differed markedly from laboratory experience.

Laboratory-derived estimates usually result from conditions carefully contrived to separate or remove effects from an otherwise complex system. But changes in spatial organization may in fact obscure relationships that are apparent in field trials. Furthermore, rates actually realized are often more meaningful to management than are optimum rates or values.

This study sought to extend an existing larch casebearer/parasite model to include resource limiting effects in the interaction by analyzing data from earlier experiments under nearly natural conditions and to develop or refine sampling procedures which would provide accurate, efficient, and reliable estimates of larch casebearer parameters under natural conditions.

Methods

Study 1: Characterizing the functional response of the parasite,

Agathis pumila, on the larch casebearer

Data from parasite rearings on trees caged with cheesecloth in 1965 were reexamined for possible inferences on Agathis attack rates. Numbers of parasites released on each tree, and estimates of larch casebearer density before parasite release and rate of parasitism after release were used to estimate the form of the functional response of the parasite (Appendix A). The sigmoid response was included in an existing biocontrol model (Appendix B).

Study 2: Sampling distributions of larch casebearer

Overwintering larch casebearer were sampled from eight stands in northern Idaho (Appendix C). Branches were removed from 2 ft intervals along the bole of the tree. Twigs consisting of the distal 20 cm of each branch comprised a sample unit. Over 392,000 sample units were examined and the number of larchcasebearer counted and recorded for each.

Earlier attempts to design an efficient sampling procedure generally assumed sample densities were distributed in a normal (gaussian) fashion. Further, consistent differences in sample means estimated by sampling from specific heights within a sample tree have not been demonstrated.

The data from this study show that, in general, differences between trees comprise a larger proportion of the sample variance than do differences between locations within trees (Table 1). Differences between locations along the bole were significant in all stands, but a "representative" stratum could not be identified consistently for sample trees. Table 2 shows that data from all plots differ markedly from normal, or gaussian, distributions.

These preliminary results suggest that an efficient sampling procedure should be designed to operate on non-normal distributions, and that samples should be removed and examined from several trees and several locations within trees. These considerations strongly indicate a sequential sampling method (Appendix C).

Recommendations

The results of these studies, especially Study 2, provide a method for rapidly monitoring a large number of stands for larch casebearer densities, rates of parasitism, and other larch casebearer associated indices. The sampling protocol should be used in conjunction with the usual sampling method until confidence in the method is acquired.

Study 1 was not as broadly based as Study 2 and still provides only as much predictive capacity, or confidence, as is provided by the basic model. Further studies on functional responses of Agathis, and perhaps other larchcasebearer parasites as well, would be desirable. Such influences as temperature, clustering or patchiness of prey, and effects of wind and light on parasite searching success should be resolved.

Table 1. Analysis of variance for larch casebearer plots.

Plot 1:

Source	DF	SS	MS
Total	1520	20185.	
Tree	12	2333.	194.
Stratum	17	1155.	68.
Error	1491	16697.	11.

Plot 2:

Total	2846	662612.	
Tree	19	69759.	3671.
Stratum	16	160335.	10021.
Error	2811	432518.	154.

Plot 3:

Total	2872	158432.	
Tree	17	22592.	1329.
Stratum	22	8982.	408.
Error	2833	126858.	45.

Plot 4:

Total	1286	9531.	
Tree	10	1024.	102.
Stratum	21	617.	29.
Error	1255	7890.	6.

Plot 5:

Total	2547	89233.	
Tree	14	5273.	377.
Stratum	16	5560.	347.
Error	2517	78400.	31.

Plot 6:

Total	1481	72864.	
Tree	10	13323.	1332.
Stratum	15	672.	45.
Error	1456	58870.	40.

Table 1. Analysis of variance (cont.)

Plot 7:

Source	DF	SS	MS
Total	3379	118165.	
Tree	19	54161.	2851.
Stratum	15	3792.	253.
Error	3345	60212.	18.

Plot 8:

Total	1000	270802.	
Tree	7	60859.	8694.
Stratum	13	80718.	6209.
Error	980	129225.	132.

Table 2. Sample statistics for eight northern Idaho larch casebearer plot. Sample measurements are the numbers of larch casebearer per 20 cm twig (about 25 spurs).

Plot	N	mean	variance	skewness	kurtosis
1	1397	3.97	13.2	1.4	2.4
2	2737	18.7	229.	1.1	1.2
3	2595	10.3	50.8	0.9	1.2
4	1117	2.4	7.8	1.7	3.2
5	2413	8.7	33.	1.0	1.6
6	1176	7.2	51.3	1.9	4.4
7	3155	3.2	36.8	3.7	17.2
8	972	17.9	270.	1.0	0.0

Control of larch casebearer populations by
density-dependent parasitism

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Abstract

In 1960, 3 years after discovery of the larch casebearer in Idaho, the U. S. Forest Service began releasing the host-specific braconid, Agathis pumila. Whether the parasitoid is controlling casebearer population densities in northern Idaho has not been conclusively demonstrated.

Data from parasitoid rearing studies suggest that the rate of attack on the casebearer increases with casebearer density, and that the functional response of the parasitoid is sigmoid in form. Such a functional response could allow the host-parasitoid system to persist indefinitely with host densities regulated at endemic levels.

Paper presented to the 51st Annual Meeting of the Northwest Scientific Association, Washington State University, Pullman, 31 March 1978. Work conducted under project 0355, Washington State University, College of Agriculture Research Center. This study was funded in part by the Intermountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture.

The larch casebearer (Coleophora laricella) is a widely distributed defoliator of most species of larch. Its occurrence in the Intermountain region was first noted in 1957 near St. Maries Idaho. The infestation spread rapidly so that by 1971 all available larch types from southern British Columbia to eastern Washington and then to western Montana exhibited at least minimal damage.

The adult moths, about a quarter of an inch in length and silvery-gray in color begin emerging in June. Hemispherical eggs are laid on larch needles; the larva hatches by mining directly into the needle from the lower side of the egg. The first and second instar larvae remain within the needle, mining down one side and up the next. The third instar larva feeds externally on the needles and carries about an empty shell of a needle to protect its soft parts, hence the name "casebearer."

Sometime in late October or early November near or just preceeding the time of deciduous needle fall, the casebearing larva moves distally along the twigs and overwinters after fastening itself securely to the twig with silk strands. In April, about the time of bud burst, the larvae molt to fourth instar and become active foliage feeders again. The relationship between time of bud burst and larval reactivation becomes important: if the developing foliage is not extensive, the large fourth instars can cause considerable damage.

The larch casebearer has several predators and parasites. One of these, the braconid Agathis pumila, was originally imported from Europe expressly as a biological control agent for larch casebearer. It has been released at about 400 sites in Idaho and several studies have been conducted to determine whether the parasite is or can be an effective control agent in the northwest. These studies have included assessing establishment of the parasite and use of

simulation models to test predicted parasite-host responses. It appears that at the present time a large sample of casebearer pupae taken from anywhere within the Intermountain region will contain some degree of parasitism by Agathis; however, this fact alone does not necessarily demonstrate that the parasite is regulating population densities of the larch casebearer.

The feeding rate of an individual predator, or in this case the oviposition rate of a parasitoid, is influenced by density of the prey or host. A simple relationship (Fig. 1) might be one in which the rate of attack increases as more prey become available until the predator's ability to process, or handle, prey becomes saturated. There may be a lower density limit, as here, below which the predator does not attack or can't find prey. This sort of relationship is called a Type II functional response. A Type I response, which we will not discuss, is that shown by a filter feeder. Type II responses are often shown by arthropod predators feeding on only one type of prey.

A Type III response (Fig. 2) is superficially similar to the Type II: as prey density increases, so does the rate of predation which then saturates at high prey densities. But at lower densities, the rate of attack decreases less rapidly than does prey density. Thus a Type III response suggests the predator is capable of regulating prey density. When prey density increases, the number of prey killed (and removed) increases rapidly thereby decreasing the number of prey available. But while prey density decreases so does the predation rate; prey escapement is higher and the numbers of prey increase again. A laboratory example of this response has been provided by Holling with shrews preying on sawfly cocoons in the presence of alternative food. Apparently the sigmoid form of the response is attributed to learning by the predator: as prey become common, the predator learns they are good to eat or acquires a searching image of the prey.

A parasite or predator may appear to regulate the population density of its host if it is capable of overwhelming extermination of the prey. In real-life situations extermination is a local phenomenon, so that groups of prey exist for short times in some areas until discovered by the predator. Laboratory examples have been illustrated by Huffaker with mites confined to oranges; an example taken from field experience is that of prickly pear cactus and the moth Cactoblastis in Australia. This strategy regulates population density near zero and can be explained with any form of functional response, provided that actual predation exceeds, for all host densities, reproduction by the prey.

It is apparent that larch casebearer are not exterminated by Agathis under natural conditions. It seems reasonable, then, to ask whether, under natural conditions, Agathis is capable of regulating casebearer densities.

In an effort to determine potential rate of increase of the parasitoid under field conditions, laboratory-reared Agathis were released on trees in which the whole crown was caged in cheesecloth. Male:female ratios varied from 11/1 in early July to 1/10 in late July. Numbers of males and females were counted out and released into the cheesecloth cages. The following summer (during pupation), the tree crowns were cut into one foot sections; a subset of all sections was selected randomly. From each sample selected, total casebearer was estimated as a product of the number of lateral braches on the sample and the average number of casebearer found on two of the branches. Twenty casebearer pupae were examined from each sample for parasitism by Agathis.

I used the same data to test whether, under conditions outside the lab, the functional response of Agathis on larch casebearer is Type III. To reduce some of the extraneous variation, I did not consider samples from trees which

had parasites released more than once or trees which didn't produce at least two sample parasite offspring.

When the number of casebearers attacked per Agathis female is plotted against the number of casebearer larvae in the cage, the high variation among trees (cages) does not clearly reveal (Figs. 3-6) whether the functional response of Agathis females to casebearer larvae is Type II or Type III. Additional evidence must be sought on which to base any conclusion.

Notice that for Type II responses, the percentage of the host population attacked decreases with increasing host density. Only for Type III responses does the percentage of the host population attacked increase with increasing host density, and then only up to a point.

Depending on the weight given to the three highly variable points, the relationship between percentage parasitism and casebearer numbers (Fig. 7) is more or less positive suggesting that the functional response is concave upward over at least some of the range of casebearer densities shown and therefore of Type III.

These observations indicate that Agathis can regulate casebearer densities, but only when the density is low to begin with or depressed by weather or artificial means. As necessary correlates we now ask whether Agathis is indeed host-specific in the northwest or whether host-specific parasitoids, in order to survive, exhibit a decreased searching efficiency at low host densities.

ATTACKED

80

40

0

20

40

60

80

100

HOST DENSITY

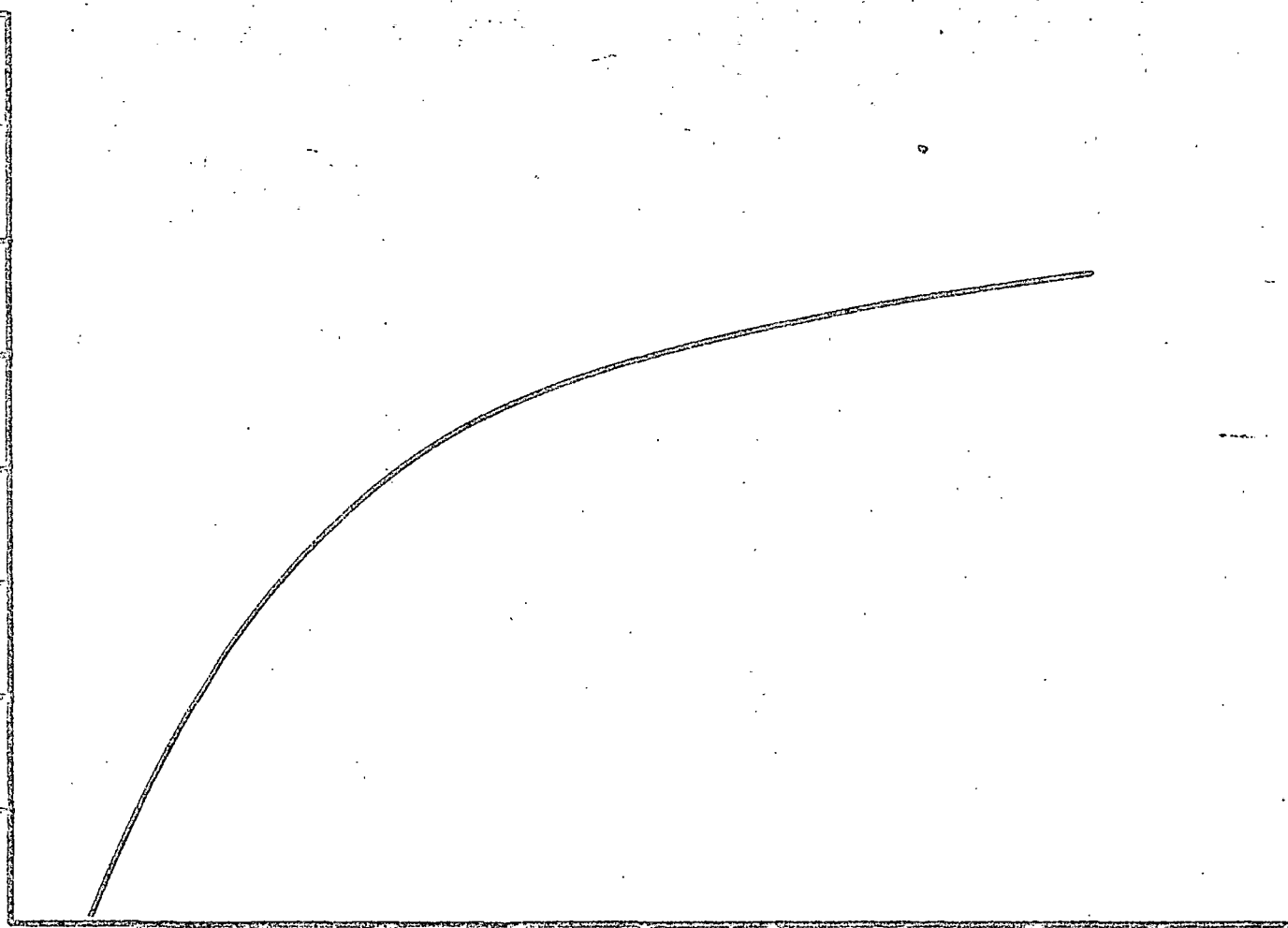


Fig. 1

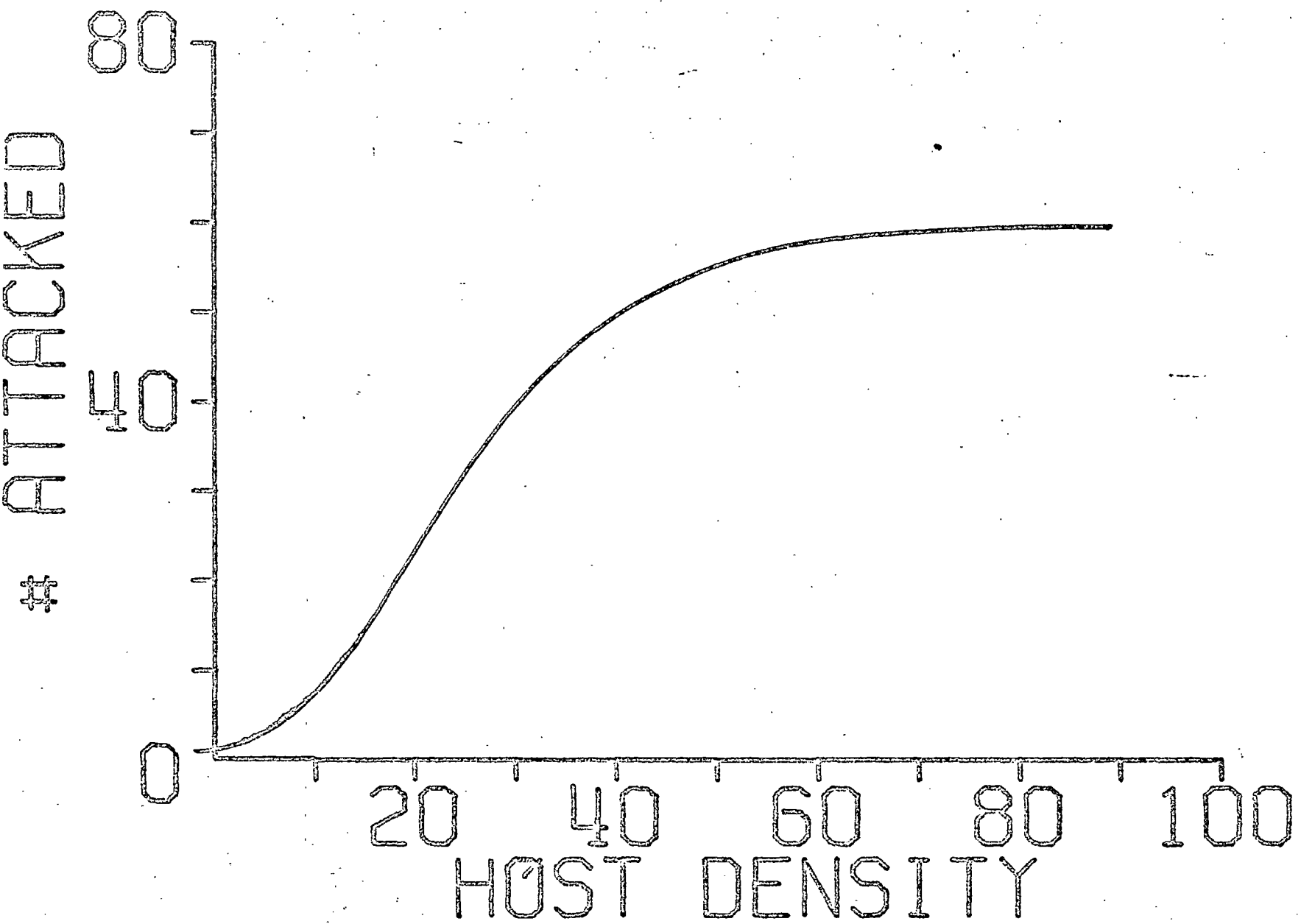
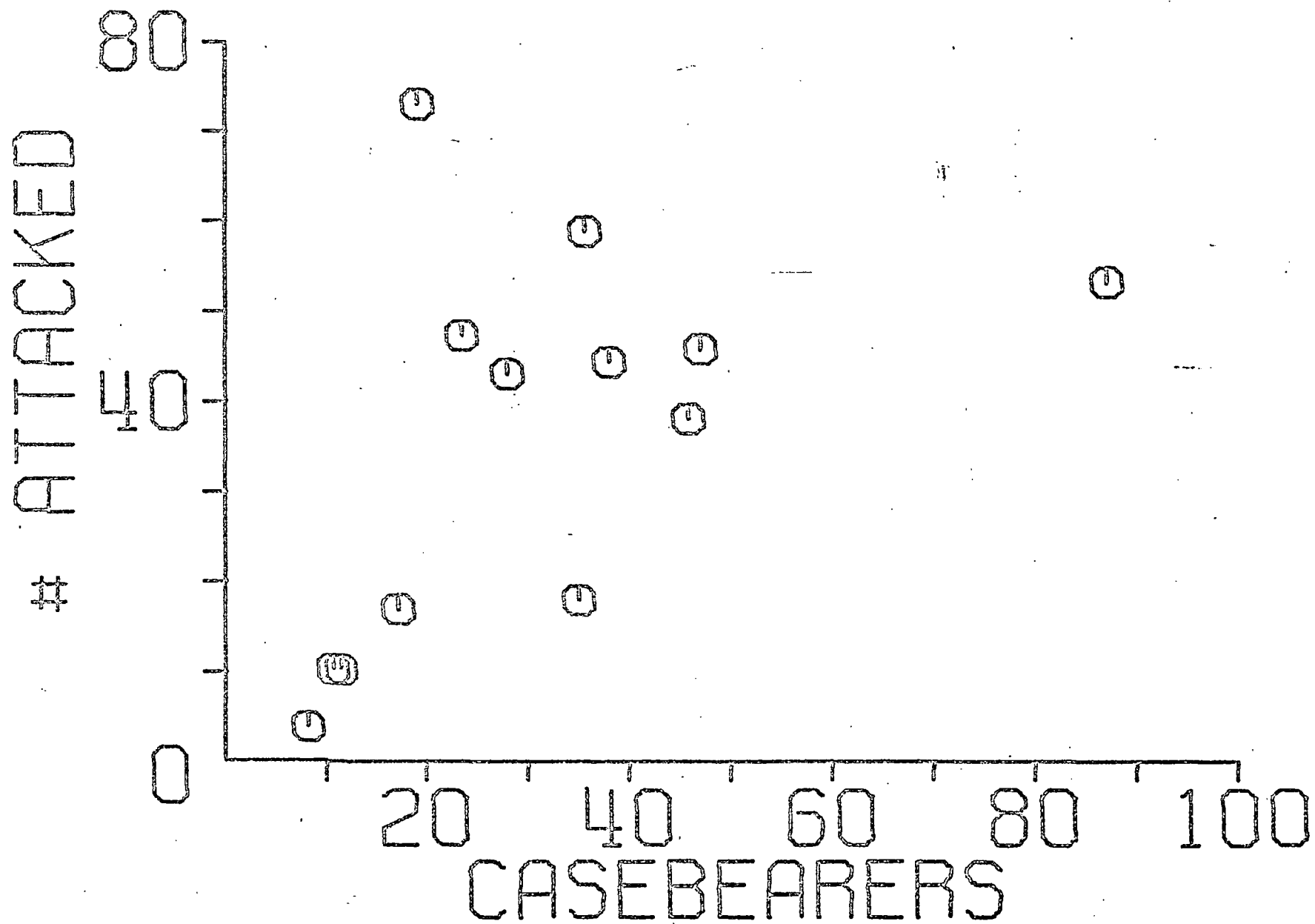


Fig 2



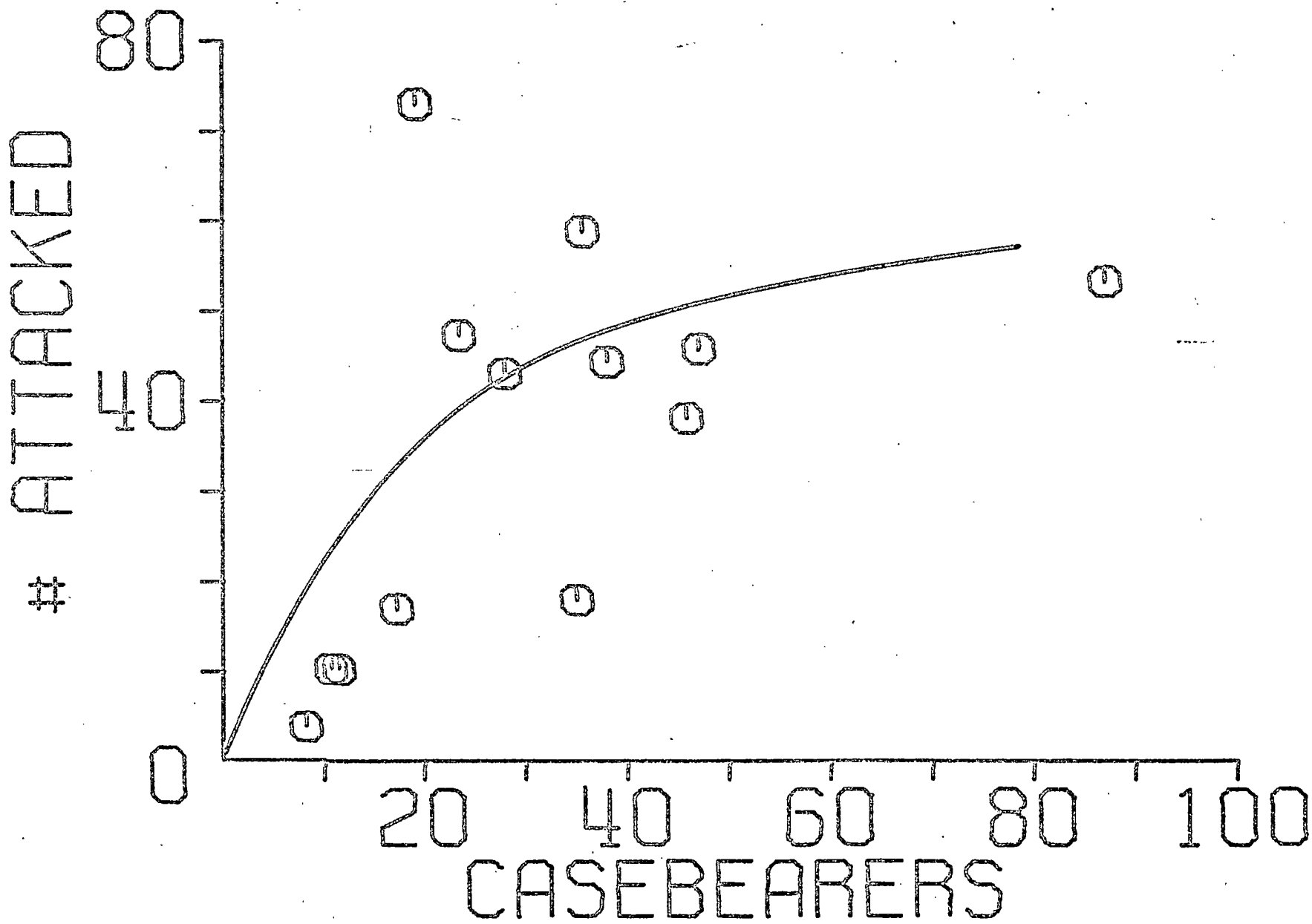
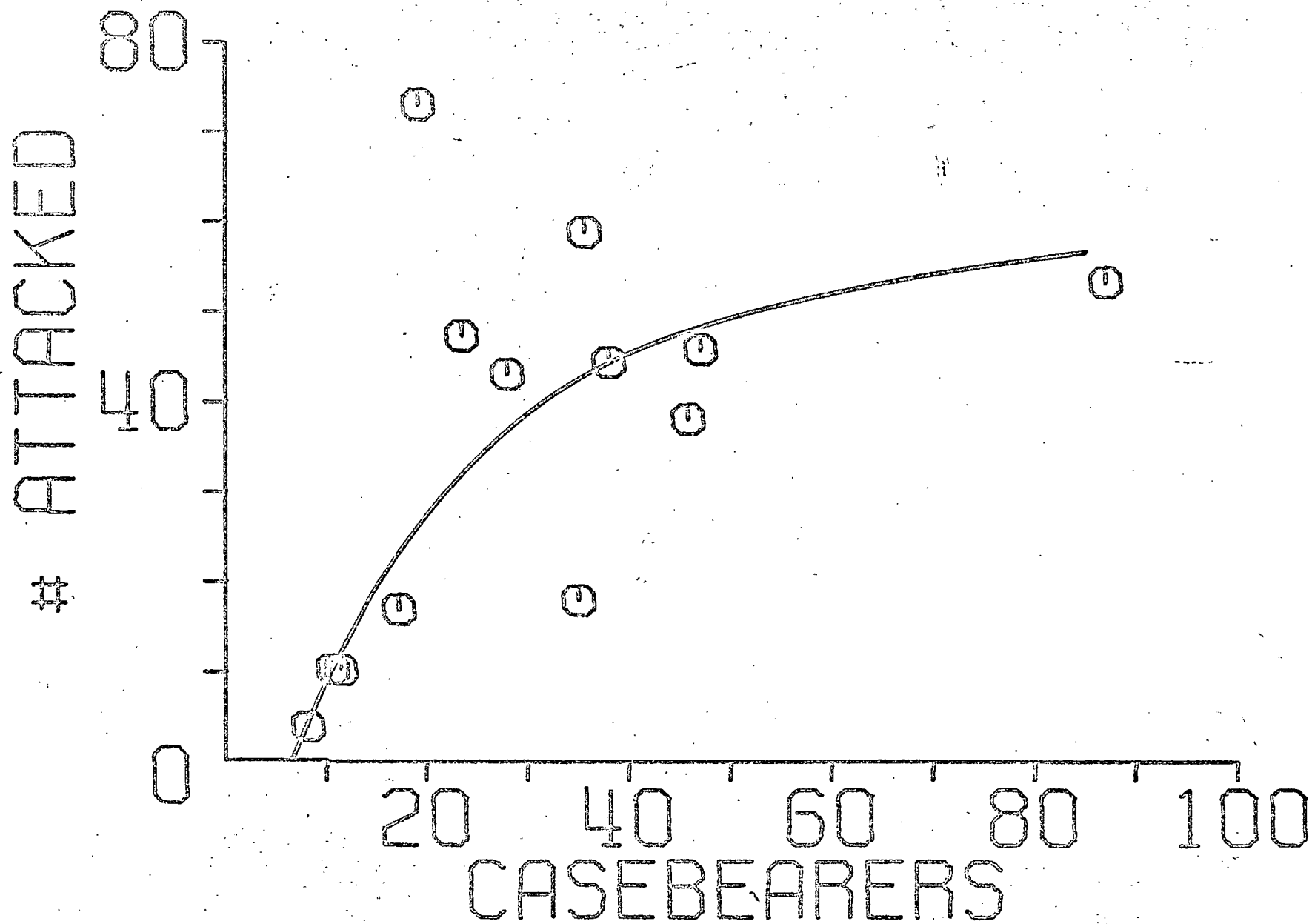


Fig 4



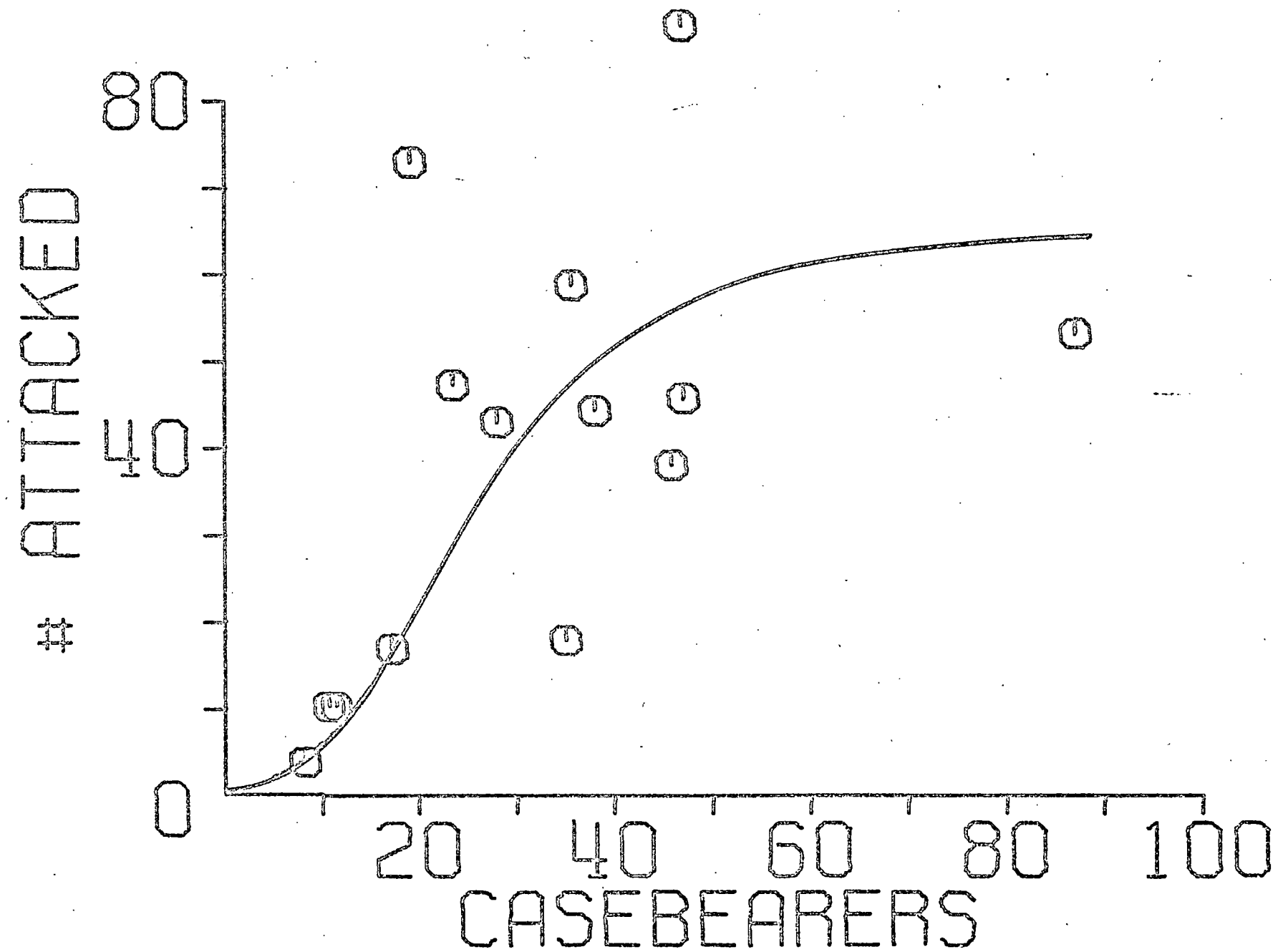


Fig 6

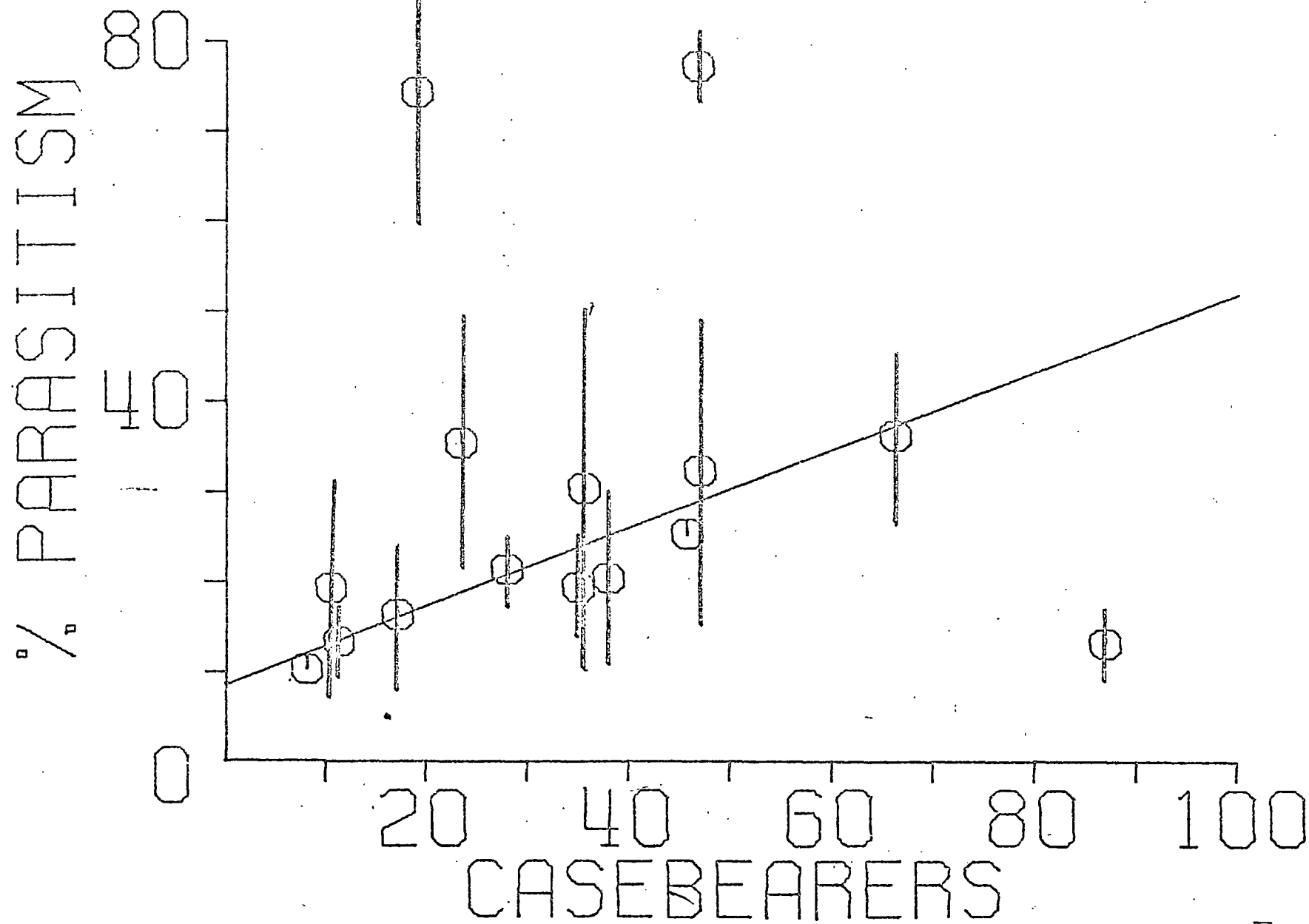


Fig 7

Modeling Spatial Heterogeneity

in Forest Pest Management

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Abstract

Simulation models are used increasingly as a basis for integrated forest management. Since forests consist of regions or stands which differ in species composition or site factors, a conventional approach has been to evaluate the model at several locations. Organisms and nutrients may then be exchanged among these locations. As the number of locations increases, the linkages among them become numerous and computationally cumbersome.

As an alternative, continuous polynomial surfaces may be fitted to the values of relevant variables at each location. The height of the surface then predicts values between locations. The mathematical properties of fourier surfaces are particularly useful and may significantly decrease the number of variables that must be retained during simulation of mobile populations.

A parasitoid-host model with fourier surfaces representing numerical values of state variables exhibits reasonable behavior in planar space.

Paper presented to the 1978 Annual Meeting of the Ecological Society of America, University of Georgia, Athens, 22 August. Work conducted under project 0355, Washington State University, College of Agriculture Research Center. This study was funded in part by the Intermountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture.

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Modeling spatial heterogeneity in forest pest management

The larch casebearer, Coleophora laricella, is an important lepidopteran defoliator of larch (Larix spp.) trees in the northern United States and Canada. Eggs are laid singly on larch foliage during mid-summer. Early instars mine the larch needles; later instars feed externally and carry about a hollowed needle for protection, hence the name casebearer. The casebearing form overwinters attached to larch twigs and resumes active feeding immediately after larch bud burst the following spring. Unchecked, the casebearer can cause severe damage especially during the spring feeding stage. In the intermountain northwest, entire stands may be severely defoliated. Losses in radial increment of infested larch trees often exceed 25%.

One control measure implemented by the U.S. Forest Service and some private timber companies has been the rearing and release of parasitoids such as braconid, Agathis pumila. Agathis appears to be a successful control agent on casebearer in the eastern U.S. and Canada. Its success in the west is less apparent in a different climate and on a different host tree.

A number of studies have been conducted to assess various aspects of the parasitoid/host/host tree relationships. Here the parasitoid is being reared on caged larch trees. From such studies we have tried to characterize the functional response of the parasitoid.⁽¹⁾

The spread of the casebearer and its parasites has been monitored in certain areas for almost two decades. These data allow us to draw inferences concerning the distances female casebearer disperse and values for population recruitment. Similarly, the spread of the parasitoid Agathis over a several year period tells us something of dispersal and recruitment in localized areas.⁽²⁾

These bits of information about the pest, its parasitoid, and effects of the pest on host trees have been combined through simulation models to present what we feel to be realistic prognoses, useful for managing infested larch stands. Some effort is being expended to couple models of insect pest/parasite dynamics to models of timber production, watershed yield, and grazing and recreational impact. But individual stands and habitats differ in many significant ways; among these, slope, aspect, and elevation combine to influence which trees can grow on a site. Of course each stand can be modeled separately, with some allowance made for transfer of information or materials between locations. But the linkages between stands can be cumbersome, especially if, say, insects disperse long distances, thereby extending neighborhood influences beyond adjacent stands.

In cooperation with the Intermountain Forest and Range Experiment Station, USDA Forest Service, we have adapted the use of mathematically defined surfaces to represent variables distributed in space.⁽³⁾ In this example, areas are rated for suitability as larch casebearer habitat. The variable is then fitted by the mathematical surface. Similarly, each other spatially distributed variable to be used in the simulation is approximated by its own surface. The dynamics of state variables are then computed according to models at points on a sample grid.

We use Fourier surfaces because the mathematical properties of the surfaces are well-known and provide computational ease of evaluation and fitting. Furthermore, the surfaces can provide adequate approximations for interpolated values even when the number of coefficients defining the surface is significantly less than the number of grid points sampled. Thus in our example, we use three surfaces, one for habitat

suitability and one each for pest and parasitoid insects. Each surface is defined by 72 coefficients while the model is evaluated at over 1100 regularly spaced sample points. The model used is basically a discrete form of the VPR Logistic model of population growth, with values of parameters taken from previously published works. (2) We compare two trials: in one, all initial parasitoids are released at a central location. In the other, an equivalent number of parasitoids are initially distributed among several release sites throughout the simulated region.

Shortly after release, high parasitoid densities are found in the vicinity of the single release site, the host population is saturated and parasitoid reproduction is limited by the availability of unparasitized host insects, not by the fecundity of the parasitoid. The multiple release strategy, by distributing available parasitoids, allows an abundance of suitable host insects and therefore parasitoid reproduction is limited only by the maximum recruitment rate of the parasitoid. Thus we expect faster parasitoid reproduction with the multiple release strategy, but with both strategies producing high parasitoid densities in areas suitable for the host insect and low parasitoid densities in areas unsuitable for the host insect.

We conclude that the efficient representation of spatial relationships by Fourier surfaces enhances the utility of resource allocation models in forest pest management.

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Sampling Distributions of Larch Casebearer

(Coleophora laricella Hbn.)

on Western Larch

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SAMPLING DISTRIBUTIONS OF LARCH CASEBEARER
(COLEOPHORA LARICELLA HBN.)
ON WESTERN LARCH^{1/}

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Scientific paper number 5136. Work conducted under project 0355, Washington State University, College of Agriculture Research Center. This study was funded in part by the Intermountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture.

Abstract

Intensive sampling of larch stands in northern Idaho shows that densities of overwintering casebearer larvae are clustered on the distal tips of branches, that there is no difference in densities of pupating larvae on roadside larch trees as opposed to larch trees interior to a stand, and that, with appropriate scaling, sample densities of overwintering and pupating larvae on the same or different plots can be compared.

The distributions of sample densities among diverse larch stands are similar enough that a standardized sequential procedure can be used to efficiently and confidently monitor predicted defoliation of the larch trees. An appropriate sampling protocol is presented.

Introduction

An estimate of population numbers or density is basic to any population study or pest monitoring program. Since the discovery in 1957 of larch casebearer (LCB) in northern Idaho (Denton and Tunnock, 1972), population densities of the larvae have been sampled by removing a few branches from each of several trees scattered throughout a stand. The number of fascicles or spur shoots and numbers of LCB on the branch were then counted and expressed per 100 spur shoots (spurs). Statistical analyses indicate a high degree of variability in estimates of population density within and among trees and suggest a large number of samples are necessary to accurately estimate LCB densities. These analyses have generally failed to show consistent differences in population densities by aspect or crown level within trees.

Webb (1957) devised a sequential sampling method based on data collected from New Brunswick over the period 1950-1956. Three crown levels and 50 trees were represented with sample LCB densities ranging from "very high" to "very low." He recognized that sample LCB numbers were distributed as a negative binomial, so the data were normalized prior to standard analysis of variance.

Among other important considerations, Webb recommended counting from the distal tip of a branch until 100 spurs had been inspected. His sequential method has not been widely adopted for sampling LCB densities on western larch, but the 100 spur basic sample has traditional use.

A recent study (Theroux and Long, 1978) has shown that for a given site the number of spurs per linear inch of twig is relatively constant. Thus it is unnecessary to count each spur on sample twigs provided the total number of inches in a sample is known. The time required to count and record a sample measurement may be reduced by fifty percent.

Overwintering larvae are easy to count during the absence of larch foliage and potentially are the most damaging life stage when they resume feeding in the spring. These larvae tend to aggregate near the distal tips of twigs and are the most conveniently monitored life stage of the insect provided that weather conditions allow access to the stand at an appropriate time.

Trends in the numbers of adult moths emerging are more closely reflected in numbers of pupating larvae. But pupae are not easily counted, being attached within the needle fascicles. Observations indicate that pupating larvae are distributed more uniformly along branches than are overwintering larvae.

Neither life stage is mobile. Thus an acceptable procedure for estimating density of one stage might, with proper scaling, be used to estimate density of the other.

For practical reasons, a moderate to large scale LCB density monitoring program which requires the collection of sample branches will necessarily be restricted to sampling branches within the reach of hand held pole pruners (less than about 8 meters above the ground level). Other considerations include that sample trees be on or near roadsides, skid trails, or other openings in the understory. The number of samples taken from a stand should be small enough that the potential damage level can be assessed on site if desired and if weather conditions permit.

However, assessment of the accuracy, precision, and bias of a particular sampling protocol requires a reliable estimate of the true mean population density. This can be achieved by intensively sampling all larch trees in a given area.

Currently, the LCB monitoring procedure practiced by the Forest Service in northern Idaho removes four branches with a pole pruner from approximately midcrown of 10 trees on a site. Then, using the information in Theroux and Long (1978) the number of linear inches required to contain 100 spurshoots is calculated. Distal portions of each branch are clipped and bagged until the required number of inches of twig is obtained. The samples are removed to the laboratory for counting.

This study

- 1) characterizes the frequency distributions of LCB density measurements from the distal tips of branches from each of several larch stands,
- 2) assesses the similarity between density estimates of pupating and overwintering larvae,
- 3) compares pupal density estimates between roadside trees and trees interior to the larch stand, and
- 4) devises and tests a method which accurately and efficiently monitors density of LCB larvae in candidate stands.

Methods

Establishing sample plots

Sample plots were established in pure and mixed, open and closed stands of larch. All plots are composed of even-aged larch trees less than about 14 meters (45 feet) in height. Sample trees comprise groups or clusters of larch with no intervening larch trees excluded. The number of trees in each plot varied from 8 to 20 depending on the density and distribution of larch stems on the site.

For a group of sample trees, plot center was arbitrarily established. Each tree was numbered; distance and bearing from plot center and diameter at breast height (DBH) were recorded.

Of 8 Idaho plots, 7 were used for sampling overwintering larvae (Fig. 1), and 1 for pupating larvae:

- 1) Felton Creek, East Moscow Mountain T40N R4W Secs. 20-21.
mixed stand, contiguous crowns, 20 trees, overwintering
- 2) Elk River, T39N R2E Sec. 2.
mixed stand, open-grown with dense shrub layer, 20 trees, overwintering
- 3) Jackson Creek, T40N R1E Sec. 4.
pure stand, contiguous crowns, 18 trees, overwintering
- 4) Four Corners, T57N R5W Sec. 17.
mixed stand, open-grown, 10 trees, pupating
- 5) Bob's Creek, T41N R1E Sec. 33.
mixed stand, open-grown, 15 trees, overwintering
- 6) Four Corners, T57N R5W Sec. 17.
mixed stand, open-grown, 11 trees, overwintering
- 7) Squaw Valley, T59N R5W Sec. 14.
pure stand, open-grown, 20 trees, overwintering
- 8) Benton Creek, PREF, T58N R4W Sec. 26.
mixed stand, all roadside, 8 trees, overwintering

Removal and collection of samples

Branches were removed from sample trees with a pole pruner. An orchard ladder was used to extend by about 3 meters (ten feet) the length of bole accessible to the pole pruner. Primary branch length removed was normally less than 60 centimeters (24 inches). Branches were removed at intervals of about 0.6 meters (2 feet) along the bole.

When branches from a particular height interval were on the ground, approximately 20 centimeters (8 inches) of each distal tip (primary, secondary, tertiary, etc.) were clipped from the branch. About 13 replicate samples from each height interval were bagged and marked by tree number and sample height.

Bagged samples from most plots were removed to Washington State University or to the Forestry Science Lab in Moscow for counting LCB larvae. Samples from plot 4 were counted at Priest River Experimental Forest, Idaho, by members of the Youth Conservation Corps.

Results

Analysis of the data base

The distributions of density measurements on 20 centimeter (8 inch) samples are summarized for each plot in Table 1. These statistics and the frequency histograms in Fig. 2 clearly support the conclusions of Webb (1957) and Moody (1977) that LCB are clustered on branches within a tree. This clustering is more apparent when LCB densities are low, since variance increases as mean density increases (Fig. 3) and obscures the LCB clusters. For a number of independent LCB sample plots, including the ones from this study, Fig. 4 relates the negative binomial parameter, k (Waters, 1959), with the mean density of LCB per twig. (The number per twig is approximately one-fourth the number per 100 spurs.) Values of the parameter range from 0.3 to 3.1 on our sites, but we have calculated values as high as 22 from unpublished data for 46 highly variable sample sites monitored since 1974.^{4/}

For plots with high population densities, kurtosis and skewness decrease and the distributions approach normality. The ratio of mean crowding (Lloyd 1967) to mean density, m^*m measures aggregation relative to density (Iwao 1972) and should be a more consistent measure of clumping than are kurtosis and skewness. The stability of the m^*m statistic (except for plot 7) suggests that LCB are clustered similarly on all plots, that the size of clusters is similar at all densities, and that the number of clusters increases with increasing LCB density.

Comparing the frequency histograms for plots 1, 4, and 7, we see that for otherwise similar distributions, plot 7 shows a remarkably high incidence of twigs with 0-1 LCB. Pielou (1969, pg. 88) has proposed an explanation for Poisson distributions with extra zeros. Plot 7 is on a wet site, was thinned recently, and many of the lower branches are draped in lichens. We speculate that a significant proportion of the twigs sampled may not have had a full 20 centimeters available for colonization by the LCB.

Relationship between density estimates of pupating and overwintering larvae

Trees of plots 4 and 6 are intermingled in one cohesive stand of larch. Of 21 trees, 11 were sampled for overwintering LCB (plot 6). The remaining 10 trees were sampled for pupating LCB (plot 4) the following June in order to compare densities estimated from the different life stages. From Table 1 we calculate the coefficients of variation ($C.V. = s/\bar{x}$) as 1.14 for the pupal plot and 0.995 for the overwintering plot. Similarly, the standard deviations of these values ($s_{C.V.} = \sqrt{\frac{C.V.}{2 \cdot n}}$) are 0.255 and 0.212, respectively. Thus the relative variation does not differ between pupal and overwintering counts and we would surmise from the relative densities on the plots that about one-third

of the number of overwintering larvae on a 20 centimeter (8 inch) twig will be found on the branch tip if the larvae are counted during pupation.

Ciesla and Bousfield (1974) described a system for rating expected defoliation by LCB. Their categories were related by extensive sampling to the average density of overwintering LCB per 100 spurs on the tree. Denton (1976) outlined a similar system and related the same categories to the numbers of pupating larvae on 100 spurs from the tree.

Another estimate of the relationship between densities of pupating and overwintering larvae can be obtained by comparing the numbers of overwintering LCB that correspond to negligible, light, moderate, and heavy defoliation levels with the numbers of pupating larvae that correspond to these same defoliation levels (Fig. 5). This ratio (0.57) is derived from many observations over a period of years but compares pupating and overwintering densities on different plots. The ratio of means on our plots 4 and 6 is 0.34 and is a better estimate of mortality during overwintering and springfeeding stages at one location during one season.

Since we know the numbers of twigs and spurs sampled, we can convert the mean density of LCB per twig to mean density of LCB per 100 spurs for each plot. Each plot of overwintering LCB was rated (Table 2) for expected defoliation according to the criteria of Ciesla and Bousfield (1974). Each mean thus calculated was converted to its pupal equivalent and then rated for defoliation according to the criteria of Denton (1976). Overwintering numbers were converted to pupal equivalents by multiplying the mean density of overwintering LCB by the slope of the line relating the Ciesla and Bousfield and the Denton studies. Defoliation ratings do not change much with the conversion, suggesting that the conversion factors have biological meaning.

Roadside versus interior trees: effects on pupal counts

An LCB monitoring scheme could be more economical if sample trees were easily accessible. To test the hypothesis that there is no difference in LCB densities between trees exposed to roadways and those sheltered within the stand, seven pairs of trees were sampled, all near Priest River Experimental Forest. The distance between the two trees of a pair was generally about 40 meters, but never exceeded 100 meters. Trees were extensively sampled throughout the crown. A pairing design test (Table 3) did not detect consistent differences between LCB densities of the two sets of trees.

Sequential sampling method for monitoring larch casebearer densities

The Ciesla and Bousfield criteria and those of Denton might be interpreted as in Table 4. Thus if the trees which comprise a plot have 3 or less LCB per twig (about 12 LCB per 100 spurs), defoliation is predicted to be negligible and the stand can be ignored for the remainder of the season. If the trees have more than 16 LCB per twig (about 48 LCB per 100 spurs) defoliation is expected to be heavy and steps must be taken to protect the stand. For LCB densities intermediate between these values predicted defoliation is neither negligible nor heavy and the stand needs to be sampled later in the season, to assess the trend in LCB density.

An accurate and efficient sampling (monitoring) method should have the following properties: it should

- 1) operate on untransformed data,
- 2) produce the desired answer with few samples, and
- 3) provide confidence intervals for the answer.

Sequential methods categorize objects into three states: good, bad, and indifferent. These methods identify the extreme states rapidly. Field

procedure would be to collect and inspect twigs, and record the numbers of LCB until density on the plot was identified as high or low, or until a predetermined number of twigs had been examined.

The number of twigs that must be examined before a conclusion is drawn is influenced by several factors, among them are confidence levels desired, values of the upper and lower boundaries of the mid-range class, shape (k -value) of the distribution, and the true mean density on the plot being sampled. Other factors held constant, the average number required would be maximum when the true plot mean was near the center of the mid-range class. If the true plot mean is not within the mid-range class, fewer samples would be required to demonstrate the fact; whatever this number may be, any stand which is not categorized after that many samples have been examined may, with known probability of error, be classified as a mid-range stand. In the following examples we have arbitrarily established the probabilities as $p < 0.05$ that a particular plot density will be incorrectly classified. The average number of samples required to classify the stand is not very sensitive to variation in k -values within the range encountered (Fig. 6).

The average number of twigs that would need to be inspected for several mid-range boundaries if the true mean density is not included in the interval is shown in Table 5. To use the table define upper and lower boundaries of the mid-range class, say 11 LCB per twig (about 44 LCB per 100 spurs) and 5 LCB per twig (about 20 LCB per 100 spurs). The width of the class is $11 - 5 = 6$ and the center is at 8. The table shows that, on the average, about 11 twigs will be examined before the stand is classified. For the mid-range class, modified from Ciesla and Bousfield (1974) of 3 to 16 LCB per twig (center 9, width 13), an average of 7 twigs is still necessary.

Prior to field sampling, the forester determines the upper and lower bounds of LCB density which define the mid-range or non-extreme state. He then constructs the parallel lines in Fig. 6 according to

x -intercept

$$a_1 = -1.28 / \log_{10} \left| \frac{1 + \frac{k}{L}}{1 + \frac{k}{U}} \right|$$

y -intercept

$$a_2 = \frac{a_1}{b}$$

slope of each line

$$b = k \log_{10} \left(\frac{k + U}{k + L} \right) / \log_{10} \left| \frac{1 + \frac{k}{L}}{1 + \frac{k}{U}} \right|$$

where

k is the negative binomial parameter,

U is the upper boundary of the mid-range class, and

L is the lower boundary of the mid-range class.

A more general discussion of these equations has been provided by Onsager (1976). Using the mid-range boundaries we inferred above, a 5% chance of error in classification, and a k -value of 1.2, Fig. 7 was constructed. A random sample of twigs from plots 2 (mean density 18.7 LCB per twig), plot 4 (mean density 2.4 LCB per twig), and plot 6 (mean density 7.2 LCB per twig) are used as examples in the figure. As each twig is inspected, the number of LCB is accumulated until one of the diagonal solid lines is crossed. For plot 2 only 3 twigs were necessary to categorize the infestation as high at the 95% confidence level; for plot 4 only 9 twigs were necessary to categorize the infestation as low. After 20 twigs plot 6 has not been categorized; indeed the cumulative number does not appear to be approaching either boundary.

Conclusions

This sampling protocol can be used to monitor LCB population densities at any desired level simply by modifying, as we have described, the center and width of the interval ^{between} ~~becomes~~ high and low density levels. Potential for significant defoliation can be rapidly assessed for many stands. It is not appropriate for monitoring densities on experimental plots where detailed time series of precise density leveles are required.

For those plots a sufficient number of individual observations must be taken to ensure narrow condfidence intervals for calculated mean values. At low mean LCB densities we note that defoliation appears to be more patchy than at higher densities (see comments at beginning of Results section) and might vary noticeably depending on the location within sample trees from which twigs are taken. Fortunately, low LCB densities imply low expected defoliation and should be apparent to the monitoring personnel without resorting to a sampling technique.

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Footnotes

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Figure Captions

- Fig. 1. Locations of larch casebearer sample plots in northern Idaho.
- Fig. 2. Frequency distributions of larch casebearer on sample twigs from each plot. Densities are expressed in numbers of casebearers per 8 inch twig, approximately one-fourth the value per 100 spurshoots.
- Fig. 3. The relationship between variance and mean density of larch casebearer per 8 inch twig from the sample plots. The relationship is probably non-linear, but even the linear regression shown accounts for 87% of the variation in calculated variance.
- Fig. 4. Values of the binomial parameter, k , a measure of dispersion calculated for several Idaho larch casebearer plots including those of this study. Values of the parameter do not appear to be related to mean casebearer density.
- Fig. 5. Comparison between numbers of pupating and overwintering larch casebearer larvae corresponding to the same level of defoliation. Data from Ciesla and Bousfield (1974) and Denton (1976).
- Fig. 6. The relationship between average sample number (ASN) required to correctly classify larch casebearer densities in a stand and the dispersion (negative binomial parameter) of samples taken from the stand.
- Fig. ⁶/~~7~~. Examples of the sequential sampling (monitoring) techniques presented in text. Results shown are actual values calculated from random samples of high (plot 2), low (plot 4), and intermediate (plot 6) density plots.

TABLE 1--Sample statistics for eight northern Idaho study plots. A sample measurement is the number of larch casebearer per twig.

Plot	twigs	spurs	mean \bar{x}	variance s^2	skewness g_1	kurtosis g_2	s^2/\bar{x}	$k^{1/}$	$I^{2/}$	$m^*/m^{3/}$
1	1397	32340	3.97	13.2	1.40	2.42	3.32	1.72	6.29	1.59
2	2737	64840	18.7	229.	1.08	1.24	12.3	1.66	29.9	1.60
3	2595	61480	10.3	50.8	0.902	1.23	4.93	2.63	14.2	1.38
4	1117	27700	2.44	7.75	1.67	3.16	3.18	1.12	4.62	1.89
5	2413	61440	8.68	33.0	1.01	1.55	3.81	3.10	11.5	1.32
6	1176	30370	7.20	51.3	1.88	4.36	7.13	1.17	13.3	1.85
7	3155	87380	3.19	36.8	3.72	17.2	11.5	0.304	13.7	4.30
8	972	26990	17.9	270.	1.00	-.0128	15.1	1.27	32.0	1.79

$\frac{1}{}$ Negative binomial parameter $k = \frac{\bar{x}}{\frac{s^2}{\bar{x}} - 1}$

$\frac{2}{}$ Morisita (1962) $I = \frac{s^2 + (\bar{x})^2}{\bar{x}} - 1$

$\frac{3}{}$ Iwao (1972) $m^*/m = \frac{\bar{x} + \frac{s^2}{\bar{x}} - 1}{\bar{x}}$

TABLE 2--Expected defoliation levels by plot. Densities of overwintering larvae are converted to pupal equivalents. The level of defoliation expected for any one plot seems to be independent of whether overwintering or pupating larvae are sampled. Densities are expressed as numbers of larvae per 100 spurshoots.

Plot	Overwintering		density	Pupal rating
	density	rating		
1	17	low	10	low
2	79	moderate	46	moderate
3	43	low	25	low
4 ^{1/}	--		--	
5	34	low	20	low
6	28	low	16	low
7	12	negligible/low ^{2/}	7	negligible
8	64	moderate	38	moderate

^{1/}no overwintering larvae sampled on plot 4.

^{2/}boundary between negligible and low is 11.6

TABLE 3--Pairing design test for differences in mean density of pupating larch casebearer on 8 inch twig samples taken from roadside trees and trees in the interior of the stand.

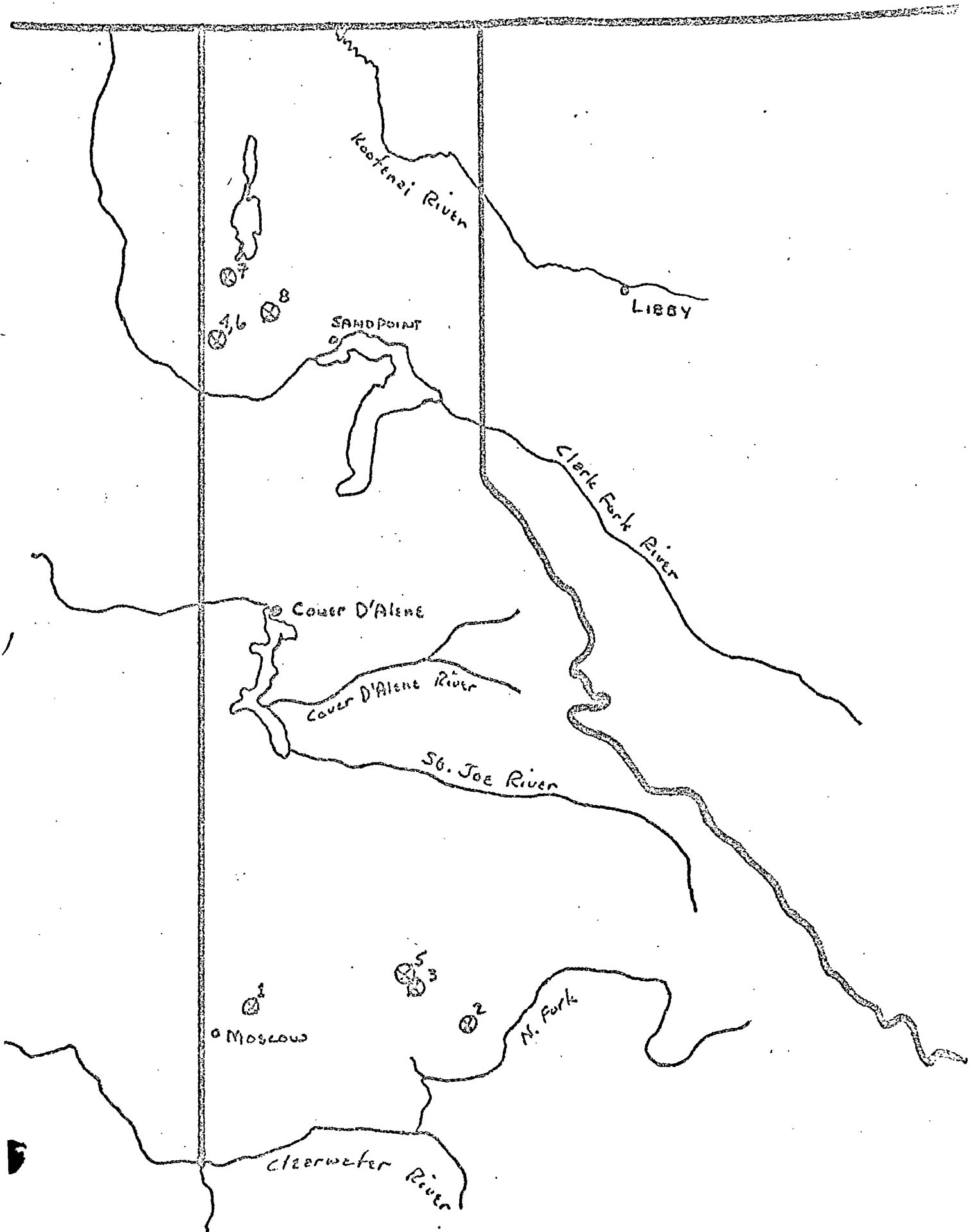
Roadside	Interior	Difference (d)	Statistics
8.54	5.58	2.96	$\Sigma d = 0.75$
7.72	12.31	-4.59	$\Sigma d^2 = 52.33$
6.85	9.96	-3.11	$n = 7$
10.08	9.43	0.65	$\bar{d} = 0.107$
6.92	5.92	1.00	$s_d^2 = 8.71$
8.27	4.93	3.34	$t = 0.0123$
11.41	10.91	0.50	$p > 0.90$

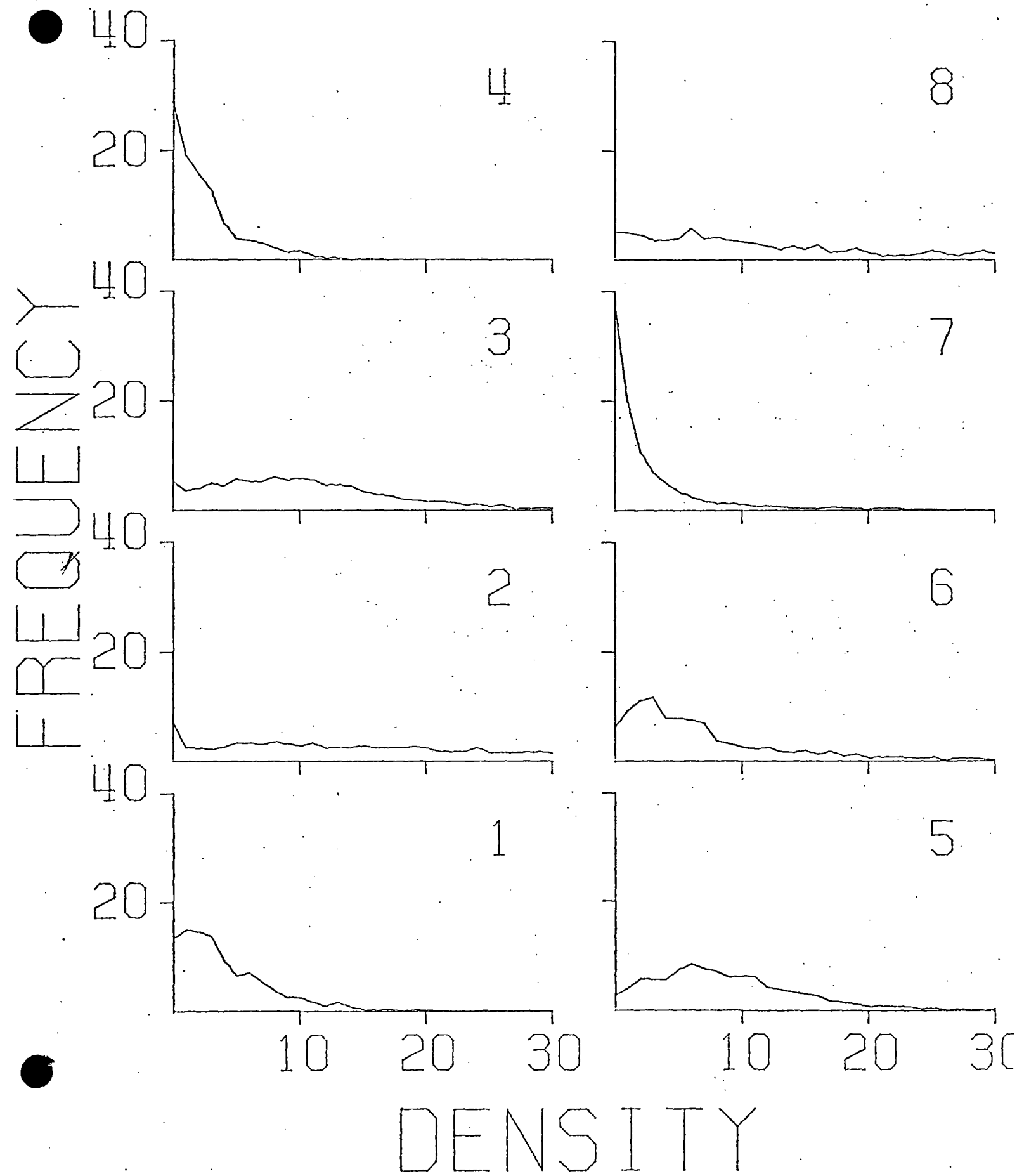
TABLE 4--Relationships between densities of larch casebearer larvae,
defoliation levels, and a prognosis of tree growth loss.

Overwintering LCB per 100 spurs	Overwintering LCB per 8 in. twig	Pupating LCB per 100 spurs	Pupating LCB per 8 in. twig	Prognosis of growth loss
0 - 11.5	0 - 3	0 - 10	0 - 3	good
11.6 - 60.4	4 - 16	11 - 30	4 - 8	indifferent
60.5 - 136.5	17 - 35	31 - 80	9 - 20	bad
over 136.5	over 35	over 80	over 20	

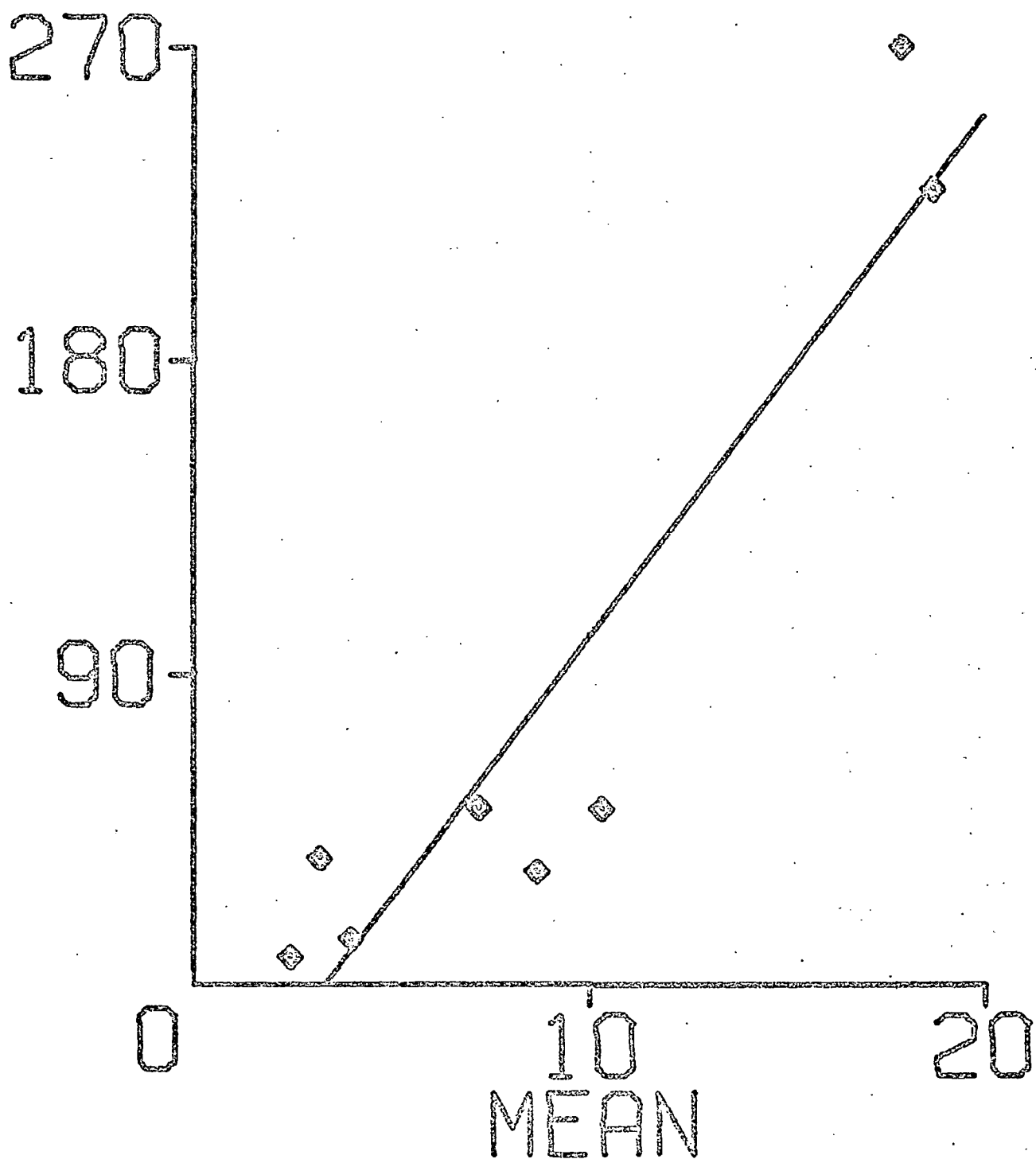
TABLE 5--Average number of 8 inch twigs that must be inspected to categorize Expected defoliation as "high" or "low" with 95% confidence. Use of the table for a particular set of economic injury levels is discussed in text.

		Center of interval							
		2	4	6	8	10	12	14	16
Width of interval	2	8	26	53	89	134	188	251	323
	4		7	14	23	35	49	65	83
	6			6	11	16	22	30	38
	8				6	9	13	17	22
	10					6	8	11	14
	12	5 or less					6	8	10
	14							6	7
	16								6

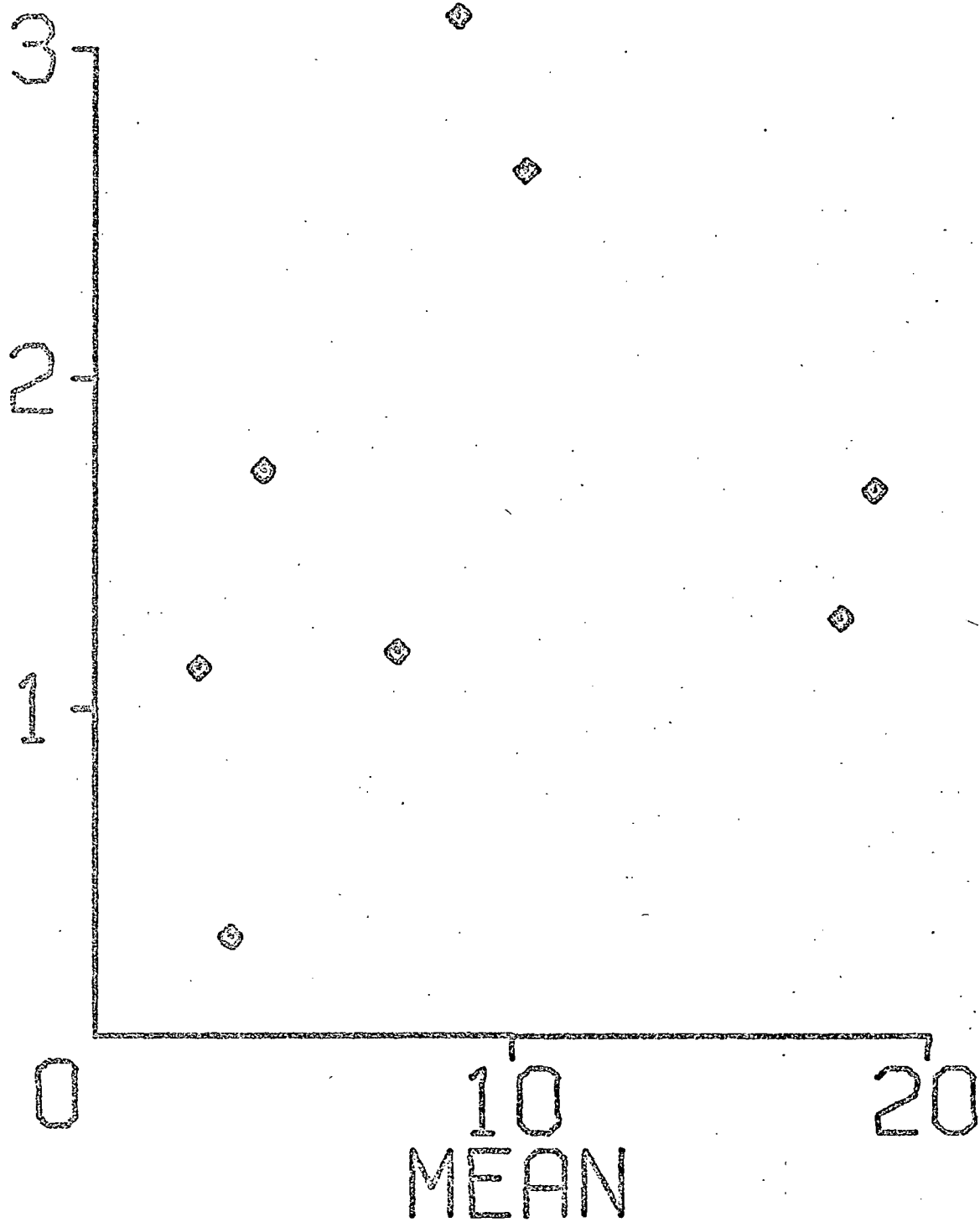




VARIANCE



DISPERSION



PUPATING

120

80

40

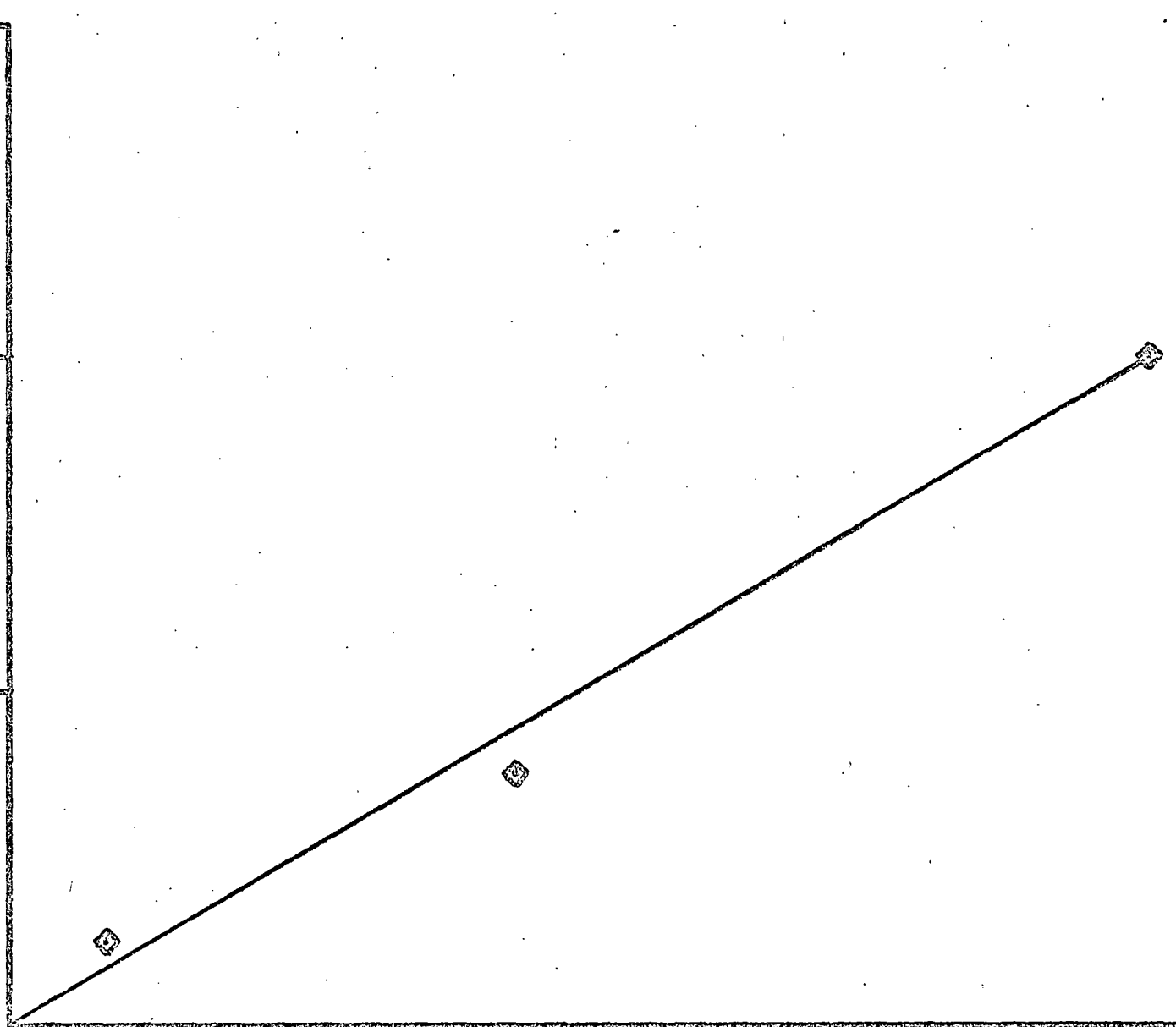
0

40

80

120

OVERWINTERING



LARVAE

